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CONTRIBUTION NO. 1, FROM THE SUBTROPICAL LABORATORY, DIVISION OF VEGETABLE PATHOLOGY, U. S. DEPARTMENT OF AGRICULTURE.

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STUDIES ON THE DISSEMINATION AND LEAF REFLEXION OF YUCCA ALOIFOLIA AND OTHER SPECIES.

BY HERBERT J. WEBBER.

The Yuccas or Spanish bayonets, since the discovery of their peculiar and unique methods of pollination, have become objects of very general interest and study. It is, however, to the long continued and painstaking researches of Drs. Engelmann,* Riley † and Trelease ‡ that we are the most indebted for the very complete information regarding this phase of the ecology of the genus which we now possess.

The methods of dissemination in the various species of Yucca, while very interesting in many features, have as yet been very little studied. The only account that has come to the writer's notice is that given by Dr. Trelease in the closing paragraphs of his paper on the "Further Studies of Yuccas and their Pollination." § Here the adaptation of the different forms of Yucca fruits to different methods of seed dissemination is mentioned, and interesting observations are given on the dissemination of *Yucca brevifolia* and certain capsular species.

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* Engelmann, Geo., "The Flower of Yucca and its Fertilization." Bull. Torr. Bot. Club, Vol. III. (1872), pp. 33–37. — "Notes on the Genus Yucca." Trans. St. Louis Acad. of Sci., Vol. III. (1873), pp. 17–54.

† Riley, C. V., "On a New Genus in the Lepidopterous Family Tineidae, with remarks on the Fertilization of Yucca." Trans. St. Louis Acad. Sci., Vol. III. (1873), pp. 55–69. — "The Yucca Moth and Yucca Pollination." Mo. Botanical Garden, 3rd Annual Report (St. Louis, 1892), pp. 99–158.

‡ Trelease, Wm., "The Nectary of Yucca." Bull. Torr. Bot. Club, Vol. XIII. (Aug., 1886), p. 135. — "Notes and Observations. I. Detail Illustrations of Yucca." Mo. Botanical Garden, 3rd Annual Report (St. Louis, 1892), pp. 161–168. — "Further Studies of Yuccas and their Pollination." Mo. Botanical Garden, 4th Annual Report (St. Louis, 1893), pp. 181–226.

§ Trelease, Wm., l. c., p. 223.

There are three types of Yucca fruits which illustrate three distinct methods of dissemination. These types of fruits were used by Dr. Engelmann to distinguish the three groups of the true Yuccas.

Sarcoyucca: — Fruits pendent, fleshy, indehiscent; seeds thick and wingless, with ruminated endosperm.

Clistoyucca: — Fruits pendent, dry and coriaceous, indehiscent; seeds thinner than in Sarcoyucca, wingless; endosperm entire.

Chaenoyucca :— Fruits erect, capsular with septicidal dehiscence; seeds strongly compressed and thin with a winged margin; endosperm entire.

The Sarcoyuccas, comprising nearly one-half of the known species of Yucca, have sweet edible fruits and are apparently well adapted for dissemination by fruit-eating animals, especially birds. In this group the seeds are usually protected by the inner part of the ovarian wall, which in the development of the fruit becomes hard and firm, suggesting in texture and functions the core of an apple. The pulp is easily removed from the core, which is more or less shaped to the seeds. This structure would suggest that the pulp only is eaten, the core and seeds being thrown away. In this case, the fruits, it would seem, were intended to be carried away by the animals eating them in order to remove the seeds from the parent plant. Birds in picking away the tender pulp would hardly reach the protected seeds but merely remove the pulp, leaving the core and seeds. This would not serve the function desired. Certain species of the Sarcoyuccas, *baccata*, *valida*, and *Guatemalensis*, having the papery core, are said by Dr. Trelease † to fall early. It is quite probable that this is a habit developed to aid in their dissemi-

* Trelease, Wm., "Notes and Observations. 7. Yucca Guatemalensis Baker." Mo. Botanical Garden, 5th Annual Report (St. Louis, 1894), p. 166.

nation. They evidently fall as soon as mature while still soft and tempting to animals. If this is so they may be gathered regularly by certain small mammals that carry them about and eat merely the pulp, discarding the core and seeds as we discard the apple core. Such animals would be prevented by the reflexed leaves from climbing the stems of the plants and securing the fruits in this manner. It is thus necessary that the fruits fall in order that they may be secured and carried off. In *Yucca aloifolia*, with which we will have most to do, this core does not occur. In the still unripe but nearly mature fruits one may get a suggestion of it in the rather firm, white membrane which immediately surrounds the seeds. As the fruit matures, however, it becomes soft throughout and this is doubtless of decided importance in its dissemination as it thus affords no resistance or hindrance to birds eating the pulp from obtaining the seeds at the same time.

In regard to the dissemination of Sarcoyuccas, Trelease * writes "These fruits are well adapted to dissemination by fruit-eating animals, especially birds, the seeds being thrown away, but I do not know of any recorded observations on their dissemination." This was the condition of our understanding of their dissemination, when in the fall of 1892 I came to Florida and was afforded opportunity to study *Y. aloifolia* in its native home. One day a mocking bird was noticed picking at the pulp of the ripe fruits and this led to an investigation of the subject of its dissemination.

The fruit of *Yucca aloifolia* (Plate 47, fig. 1) is elongated elliptical in outline, with usually a slight central constriction, though this is by no means always the case. They sometimes reach a length of 15 centimeters but are usually from 8 to 10 centimeters long. In cross section (Plate 47, fig. 2) the fruit is hexagonal in shape, caused by the spreading of the nectar grooves in the ripening of the fruit. The openings of the septal nectaries may be seen

* Trelease, Wm., "Further Studies of Yuccas and their Pollination," l. c., p. 224.

in the upper portion of the ripe fruit on which the three lobed style remains plainly distinguishable, merely having slightly increased in size during the growth of the fruit (see Plate 47, fig. 1). The fruit is fleshy throughout with no indication of a core when fully mature.

In ripening, the fruit passes from green to purple and finally to dark purple or almost black in age. The pulp, which is very tender, is of a characteristic sweetish-bitter taste. The bitter principle is not evident for a few seconds after tasting the fruit; but like that of the Indian turnip, though not so strong, soon makes itself known and persists for a considerable time. Dr. Trelease* quotes Mr. Burbidge as having characterized the taste as resembling a mixture of black currant jam and quinine. The fruits vary somewhat in taste, some being quite pleasant and agreeable. A careful selection of the fruits for a number of years would, I think without question, result in developing valuable edible varieties. The fruits, it is said, are sometimes eaten by man. They, however, are surely not much sought and man only aids in their dissemination incidentally, spreading the plant by cultivating it as a showy garden perennial. It is popularly reported that people are occasionally made sick by eating the fruits.

Extended observations through three seasons have fully confirmed the fact that the mocking bird (*Mimus polyglottus*) is a very important factor in *aloifolia* dissemination, especially in what may be termed long distance dissemination. The mocking bird is very abundant throughout the range of *aloifolia* and may be the only animal disseminator of this species. At least I have not been able to observe any other bird or animal eating its fruits. It is not improbable that the fruit of *aloifolia* has become especially adapted for dissemination by the mocking bird or some small bird of similar habits. The core which occurs in all other baccate fruited Yuccas known to the author,

* Trelease, Wm., "Notes and Observations. 7. *Yucca Guatemalensis* Baker," l. c., p. 166.

would be fatal to dissemination by birds of this size and nature.

Numerous fruiting plants of *aloifolia* have been examined and, in almost every case, some or all of the fruits were found to be somewhat eaten. Sometimes only a small portion of the pulp will be eaten, but again a large part of the fruit will have been removed.

The seeds of *aloifolia* are comparatively thick, being usually from 2 to 2.5 millimeters, and have a narrow two-edged rim (Plate 47, fig. 4). They are blackish, nearly the color of the pulp, and lie imbedded in this tender substance but a short distance below the surface. The birds in picking off portions of the pulp, which is apparently a delicate morsel for them, soon come to the seeds. These they evidently do not want, but in their greediness they cannot avoid swallowing some of them. The birds, while usually quite shy, may yet with a little perseverance be observed in all the details of feeding. As portions of the pulp are deftly picked off, frequently a seed will adhere to the bill by the surrounding sticky pulp. Many times I have seen the birds throw off these seeds by a sidewise jerk of the head as a chicken does in trying to remove dirt or hair from its bill. This results in throwing the seeds to a considerable distance, frequently from 1 to 2 meters. Many of the seeds taken with the pulp are apparently swallowed. All of the seeds removed from the fruits through the agency of the birds are not thrown to a distance in this manner or swallowed, but many of them are merely loosened and drop down into the compact rosette of erect leaves below. These either adhere to the leaves by the sticky pulp surrounding them or, if dry, roll down the leaves to the stem where they are effectually lodged. All over the upper portion of the plant in this stage, portions of the pulp are scattered, which were accidentally thrown off with the seeds or dropped by the birds in eating. These portions frequently contain seeds.

While the fruits of *aloifolia* are in this bird-disseminat-

ing stage the leaves immediately below the fruit cluster are erect, that is, point upward forming an angle of from 30° to 60° with the stem. They are linear lanceolate and rigid with sharp horny end spines, and are usually from 35 to 65 centimeters long by from 3 to 5 centimeters wide. They are very numerous and suddenly broaden out at the base, greatly overlapping each other, so that an almost closed cup is formed at the apex where the fruit cluster is borne. The most of those seeds which fall, not being twitched off by the bird, strike some one of the numerous upper leaves and adhere until the rain washes them down to the stem where they are held till a later stage of development when the upper cluster of leaves, which are now erect, have become reflexed. This stage will be described in detail later.

Many of the seeds are evidently swallowed by the mocking birds with the surrounding pulp. In this case, as in the majority of pulpy fruits, the seeds are swallowed uninjured and resist the action of digestion so that they pass through the alimentary canal and are evacuated in good condition for germination. Mocking bird dung, which had fallen on the Yucca plants, was examined in many cases and frequently found to contain *aloifolia* seeds apparently uninjured.

The stomachs of several mocking birds were examined, but, although in three cases almost the entire contents of the stomach was composed of the pulp of *aloifolia*, no seeds were discovered.

Having at my home a captured mocking bird I tested him with *aloifolia* fruits and seeds. He had become quite tame and had learned to pick flies from one's finger. I first took single seeds surrounded by some pulp. These he greedily picked from my finger and swallowed without difficulty. During the feeding several seeds were snapped from his bill, and several were thrown off by a twitch of the head in trying to free the pulp from the seeds. These actions correspond exactly with those previously observed in the field. The number of seeds swallowed was

counted. One seed made the passage of the alimentary canal and was evacuated in fifteen minutes after the first seeds were swallowed. At the end of an hour all of the seeds which were swallowed had been evacuated. The next day I gave the bird fifteen *aloifolia* seeds from my finger at one feeding. In half an hour thirteen of these had been evacuated and the others were evacuated before the end of the hour.

I next gave the bird an entire fruit and watched him pick off portions of the pulp, occasionally getting a seed. The cage previous to this had been thoroughly cleaned. During about four hours, the time he was given access to the fruit, he ate and evacuated fifty-one seeds.

All of the details of the feeding were watched many times with this tame bird and the important features of the feeding, snapping and twitching the seeds, etc., were found to correspond entirely with what had been observed in the field.

The seeds which were evacuated were apparently in good condition, but to surely determine this a number of them were planted. A very fair percentage of these germinated and formed healthy young plants.

During the fall and winter, from November to February, when the *aloifolia* fruits are ripening in greatest abundance and are suitable, they apparently form the main food of the mocking birds, judging from the frequency with which one observes them feeding on the *aloifolia* fruits, and from their excrement at this season of the year. In early fall, during September and October, many *aloifolia* fruits ripen, but at this season of the year the poke berry (*Phytolacca decandra*) and the wild and cultivated persimmons are conspicuous rivals as mocking bird food. By the middle of November these are principally gone, however, or remain as dried fragments. The fruits of *Duranta Plumieri* Jacq. and *Melia Azederach* L. play some part in supplying food for the mocking bird in late fall and winter.

While the fruits of *aloifolia* are almost always more or

less eaten by the mocking birds, and many seeds removed, yet by far the larger portion of the fruit with its contained seeds usually remains still hanging on the old fruit cluster. The pulp of the fruit gradually dries up and shortly but little remains of the heavy pulpy fruit but a light mass of seeds cemented together by the dried up pulp. The breaking of the epidermis and eating here and there on a fruit by the mocking birds greatly hastens this drying. As the fruits dry they pass the stage when birds aid in their dissemination and now a secondary method of local dissemination begins to act.

As the lower fruits of the cluster in *Yucca aloifolia* reach maturity, one or more, seldom two or even three, lateral buds, start up near the base of the peduncle and prolong the growth of the stem. A single bud soon simulates the continuation of the main axis. Several buds form a branched trunk.

In every case examined the bud or buds appear to develop from the axil of a leaf about one series below the inflorescence, and in its development the bud quite uniformly splits the base of the leaf which is directly above it. This is somewhat at variance with the observations of Dr. Mellichamp * who found the bud of *aloifolia* to spring from exactly the uppermost axil, at the base of the inflorescence.

The new rapidly growing shoot, which develops from this bud, grows up within the circle of mature leaves beside the old fruit cluster (Plates 45 and 46); which is pushed to one side by the growth of this secondary branch, which in turn bears an inflorescence.

Whether the inflorescence of Yucca is truly terminal, morphologically speaking, and the bud lateral, I have not yet been able to determine. Engelmann † speaks of the inflorescence of Yucca as terminal; and Trelease mentions

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* Quoted by Dr. Engelmann in his "Notes on the Genus Yucca." Trans. St. Louis Acad. Sci. III. (1873), p. 22.

† Engelmann, Geo., "Notes on the Genus Yucca," p. 25. Reprinted in "The Botanical Works of Geo. Engelmann," p. 282.

the inflorescence of *Yucca brevifolia* as terminal: "After blooming, two or three stout branches usually develop by the side of the original apex, which now has ended its growth. When these have reached a length of two or three feet each forms a *terminal* inflorescence and branches in its turn, giving rise to a repeated forking or tripartition." * It does not appear, however, that a morphological examination has been made to determine this point. In the lack of definite information, I speak of the inflorescence as terminal and the buds as lateral in this paper.

The periodical development from the base of the inflorescence, of the lateral buds which continue the stem in *aloifolia* and some other Yuccas, results in forming a trunk consisting of a certain number of units or segments which are quite distinct. These may be designated ecological phytomers or *phytomeroids*.† The branches formed at the side of the old fruit cluster do not usually bloom the next spring, but spend a year in their development, bloom the second spring, and fruit the second fall or winter after they start to develop. A period of two years is thus required for the completion of one of the phytomeroids. No exceptions to this have been observed though they probably occur. Some plants bloom very early in the spring and mature their fruits early in September. It is quite probable that the lateral shoots of these early blooming plants may succeed in making a sufficient growth to bloom the next spring, probably rather late, and mature their fruits the next

* Trelease, Wm., "Further Studies of Yuccas and their Pollination," l. c., p. 194.

† From phytomera (*φυτον*, plant and *μερος*, part) and *ειδος*, form Phytomera or phytomers was used by Gray (Gray's Botanical Text Book, 6th Ed., Vol. I., Structural Botany or Organography on the Basis of Morphology, p. 7), to designate the units of a stem, each including an internode and node with its leaf.

Phytomeroid as used here is apparently equivalent to what Gray has called *definite shoots* (l. c. p. 49), and is what in German is known as *Langtrieb*, *Haupttrieb*, etc. (R. Hartig, "Lehrbuch der Anatomie und Physiologie der Pflanzen," p. 116. Pax, "Allgemeine Morphologie der Pflanzen," p. 24.)

winter. I am satisfied, however, that this is not frequently the case. It is probable that certain branches may also require more than two years for their development before fruiting. I am inclined to think this not uncommon though no specimens under continuous observation have been known to do so.

One of the most marked and peculiar characters of *Yucca aloifolia* and a number of other Yuccas is the reflexing of the leaves. The reflexing does not take place gradually as the leaves are formed, but corresponds with the phytomeroids of the stem mentioned above. Only the leaves belonging to the upper phytomeroid are erect, those of the preceding older phytomeroids are all reflexed more or less strongly, becoming more and more closely appressed to the stem the nearer they are located to the base. All of the leaves belonging to a certain phytomeroid become reflexed at the same time, and this reflexing takes place at a certain stage in the development of the fruit and lateral shoot. About the time that the lateral shoot or shoots which form at the base of the old fruit cluster start their development, the leaves of the upper phytomeroid to which the old fruit cluster belongs, begin slowly to reflex. As the lateral shoot develops they become more and more strongly reflexed till by the time the lateral shoot is half grown they have in most cases come to point strongly downward and form an angle of scme 45° or less with the stem (Plates 45 and 46). This angle grows less and less each year until the leaves have become closely appressed to the trunk. They finally die and dry up, but remain persistent, clothing the lower portion of the trunk (Plate 46). In cultivated *aloifolia* these are usually pulled off to render the plants more sightly, a practice liable to cause a misunderstanding of the true habit of the plant unless this is remembered.

The leaves of the lateral shoots which start at the base of the old inflorescence, remain rigid and erect all through their growth and during flowering, as long, indeed, as these

lateral shoots form the uppermost phytomeroid. As the fruits which they bear ripen and lateral buds in turn start at the base of their fruit stems, they cease to be the terminal phytomeroids and their leaves begin to reflex.

The leaves of the upper phytomeroid while in the erect stage are separated by a wide angle of divergence from the reflexed leaves of the preceding phytomeroid, the point of divergence being usually very marked (Plates 45 and 46).

The phytomeroids of the trunk are usually from one to two feet in length and easily distinguishable even in the old lower growths. A slight swelling in the trunk frequently marks the place where one growth ended and the next began.

The reflexing of the leaves is evidently due to a strong epinastic growth of the tissue at the base of the leaf. The tissue on the under surface at this point collapses under the pressure exerted and becomes somewhat wrinkled.

The time occupied in the reflexing of the leaves of a phytomeroid varies considerably. The first marked reflexing takes place quite rapidly, but the gradual drying and compressing against the stem is a slow action, running through several years. On starting to reflex, the leaves pass below the horizontal and come to point downward in from one to three months. After becoming reflexed, the leaves remain fresh and apparently active through the development of about two other phytomeroids, after which they begin to dry up and finally die. The length of time which they remain living apparently depends largely upon the conditions to which the plant is exposed. Plants growing on the sterile sand dunes along the coast or in old neglected yards usually have very short leaves, which after reflexing live only for a short period. Usually all leaves are found to be dried up in such cases except those on the two upper phytomeroids. Occasionally only those of the uppermost phytomeroid will be found perfectly fresh and

active, the leaves beginning to dry up as soon as they become reflexed. In plants grown in rich soils or in well manured yards, the leaves of two or three phytomeroids may frequently be found green and apparently active.

While the reflexing of the leaves in *Yucca aloifolia* is probably not primarily to serve as an aid in seed dissemination it is yet certain that it is of considerable service in this direction. The seeds which are dislodged by the mocking birds in feeding, as described above, being heavy fall into the crown of still erect leaves below, where they usually adhere to some one of the numerous leaves or slide down to the apex of the stem where the almost closed cup formed by the broad bases of the leaves effectually arrests and retains them until a later period of development when these leaves become reflexed. If on the contrary the falling seeds rattle through the cluster of erect leaves of the upper phytomeroid, on reaching the upper reflexed leaves of the lower phytomeroid which point downward and outward, they are shot outward by these, the force of the fall serving to throw them to a considerable distance from the parent plant.

When the leaves of the upper phytomeroid, that bearing the fruit cluster, have become reflexed, the seeds which have been lodged in the cup formed by these before their reflexion, are gradually dislodged and are thrown outward by the reflexed leaves as they fall. Many may be dislodged by rain and washed downward but can hardly fail to be thrown outward as far as the ends of the leaves of the parent plant. Those seeds which fall when dry are frequently thrown outward to a considerable distance. The majority of them strike the ground from one to one and one-half meters distant from the base of the parent plant. This distance depends on the height of the plant and the angle to which the leaves are reflexed. I have examined some typical but exceptional cases, where the seeds could noticeably be seen to form a circle around the

plant at a distance of about a meter, having been thrown there in falling by the action of the reflexed leaves.

While this is not the main method of dissemination, I think that it may reasonably be claimed to form a secondary method of considerable importance.

After reaching maturity the fruits remain fresh and soft for a few weeks but gradually dry up until nothing remains but a dried fragment of the pulp which cements the seeds together into a small light mass. Long before they have reached this thoroughly dry condition they have passed the stage when the birds will eat them. Sometimes the dried fruits are broken off as a whole and these, falling, strike the reflexed leaves and are thrown outward to some distance as they fall to the ground. The fruits may now be knocked about by man or animals or may become disintegrated in the place where they fall. This would also serve to disseminate the seeds to some extent. Many of the seeds still remain sound and evidently capable of germination.

A still more peculiar aid to dissemination is found in the larvæ of the Bogus Yucca Moth (*Prodoxus decipiens* Riley) which is very common here and probably throughout the *aloifolia* region.

The eggs of *Prodoxus* are deposited principally in the young flower stem, though it is said by Riley * that they are also found frequently breeding in the fruits of the indehiscent Yuccas like *aloifolia*. I have never observed them in the fruits of *aloifolia*, though I have made no special attempt to find them. The incision on the young peduncle made by the ovipositor leaves a discoloration and forms ultimately a sort of cicatrice which remains distinctly visible and as the stem dries becomes slightly elevated (Plate 47, fig. 3, b). The larva burrows in the tissue of the peduncle, molts according to Riley three times, and acquires full growth in a month. "It prepares for hibernation in the autumn, a cocoon of white

* Riley, C. V., "Yucca Moth and Yucca Pollination," Mo. Bot. Garden, 3d Annual Report (St. Louis, 1892), p. 128.

silk which is covered on the outside with castings and which remains protected within the stem. Before making the cocoon, however, it generally eats a passage way to the outer covering of the stem and lines this with silk leaving but a thin cap.'' During the time that the fruits are drying up, as described above, the larvæ of *Prodoxus* are particularly active and in many cases their burrowing succeeds in cutting the peduncle entirely off so that the fruit cluster falls to the ground. I have seen many clusters cut off in more than one place so that they are separated into several fragments. These portions of the fruit cluster may each retain attached a number of the old more or less dried up fruits containing many good seeds. As the fragments of the fruit cluster fall they are not lodged in the leaves as they undoubtedly would be if these remained erect; but are directed outward so that they fall, as we have seen that the seeds and single fruits do, on the ground a short distance away from the parent plant. The dried fruits are very light and the cluster with the protruding pedicels of the old flowers, is easily caught and dragged about by animals or man. Many of the seeds may be disseminated in this way.

The lateral branch which shoots forth at the base of the fruit cluster, starting its growth about the time that the fruits ripen, grows rapidly and by the time the fruits have passed the bird stage and approached the stage when the cluster is commonly cut off by the *Prodoxus* larvæ, the growth of the lateral branch has pushed the fruit cluster considerably to one side. By this time the leaves of the phytomeroid which bore the fruit cluster have usually reflexed below the horizontal so that they allow the old fruit cluster, when cut off, to fall to the ground without resistance or hindrance and direct it outward and away from the parent plant as it falls.

The cut end of the peduncle is usually smooth, showing that the cut was extended entirely across the stem with the exception of a very thin portion on the outside. This is

evidently partially cut through and that which remains is dry and brittle and breaks off by the weight of the cluster (Plate 47, fig. 3, a).

The seeds of the old dried fruits are frequently injured by the ravages of a beetle which burrows in the dried pulp and seeds. Many of the seeds, however, remain uninjured and apparently long retain their power of germination.

It is probable that the other *Sarcoyuccas* show the same leaf reflexion that occurs in *aloifolia*, but the periods of growth and other details may vary. So far as can be determined from photographs and drawings of the various species of Yucca, it appears that of the *Sarcoyuccas*, *baccata*,* *Guatemalensis*,† *Schottii*,‡ *australis* § and *macrocarpa* ‖ show this periodic leaf reflexing. Other species may show the same phenomena but no data are at hand from which this can be determined.

Of the *Clistoyuccas*, *brevifolia* ¶ evidently shows beautifully this periodic leaf reflexing, the old trunk remaining covered by the persistent, reflexed, dried up leaves which in age become closely appressed against the trunk.

Among the *Chaenoyuccas*, *Y. elata*, a stemmed species which grows to a considerable height forming a rather large tree in Arizona, is particularly interesting from the fact that here among the capsular Yuccas according to Dr. Trelease ** we find a counterpart of *aloifolia* in that the

* Trelease, Wm., "Notes and Observations. 1. Detail Illustrations, of Yucca," l. c., Plate 2.

† Trelease, "Further Studies of Yuccas and their Pollination," l. c., Plates 1 and 2.

‡ Trelease, as in last citation, Plate 3.

§ Trelease, as in last citation, Plates 4 and 5.

‖ Merriam, C. Hart, "Notes on the Geographical and Vertical Distribution of Cactuses, Yuccas, and Agave, in the Deserts and Desert Ranges of Southern California, Southern Nevada, Northwestern Arizona and Southwestern Utah." In "The Death Valley Expedition; A Biological Survey of Parts of California, Nevada, Arizona, and Utah. Part II," North American Fauna, No. 7, p. 358, Plate 14.

¶ Trelease, as above, Plates 6, 7 and 8.

** Trelease, Wm., "Further Studies of Yuccas and their Pollination," l. c., p. 202, Plate 10.— Also "Detail Illustrations of Yucca," l. c., Plate 9.

leaves become reflexed and persist on the lower portion of the trunk, becoming dry and closely appressed. The prolongation of the trunk is also by lateral buds springing from a point near the base of the peduncle. This species has a much longer peduncle than any of the *Sarcoyuccas* known to the writer and the inflorescence and fruit cluster are raised considerably above the leaves so that these apparently do not aid or interfere in any way in the dissemination of the seeds. If this species is modified for wind dissemination, as is the case with most capsular Yuccas, this elevation of the fruit cluster on a long peduncle would be of decided advantage.

The ecological significance of leaf reflexion in *aloifolia* and other Yuccas is not very evident. Prof. Lester F. Ward * has suggested that the reflexing of the leaves in the succulent fruited Yuccas has for its function the protection of the sweet pulpy fruits from the ravages of small animals such as the raccoon, opossum, rodents, etc., which might injure the seeds if the fruits were eaten by them. Any animal attempting to climb the trunk of *aloifolia* or other species having these reflexed leaves, meets an almost impenetrable barrier in the numerous sharp spines of the stiff reflexed leaves which cover the older portions of the trunk, pointing downward like so many bayonets. Should they attempt to reach the cluster of fruits by jumping up from below in the case of low plants, or by jumping down on them from neighboring trees, they are met by the rigid points of the erect leaves of the upper phytomeroid, which remain erect till the fruits begin to dry up and pass their desirability.

Dr. Trelease † mentions having found fruits of *baccata* in the crown of leaves where they had fallen on maturity and had remained protected from rodents by the reflexed leaves.

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* In a paper read before the Washington Biological Club.— Unpublished.

† Trelease, "Further Studies of Yuccas," l. c., p. 186.

As the leaves of this phytomeroid become reflexed these fruits would be freed and fall to the ground.

Dr. Merriam * mentions the reflexed leaves of *arborescens* (*brevifolia*) as effectually preventing most animals from climbing up the trunk from below. Dr. Merriam informs me, however, that the wood rat succeeds in ascending the trunk. I quote the following from a letter of February 6th, 1894: "Mr. Vernon Bailey and I have examined many trunks of the tree Yucca (*Y. arborescens*) which had been ascended by a small desert mammal known as the wood rat (*Neotoma Mexicana*). The wood rats cut off the leaves of the Yucca at the base and thus form a spiral groove or ladder around the trunk. The leaves are used by the rats in the construction of their bulky nests which are commonly made up of spiny materials such as sharp splinters of rock, parts of cactus, leaves of Yuccas, branches of spiny desert shrubs and the like. The heaps of rubbish thus formed over the mouths of their burrows constitute a protection against coyotes and other enemies." This wood rat which is the only animal known to ascend the Yucca trunk, may not have as its main object the fruits to be found there. Dr. Merriam informs me that he has found freshly cut leaves at a time when there were no fruits on the plant. They may merely desire the leaves for their nests or may feed on the tissue of the base of the leaf.

The habit of certain of the cored species of *Sarcoyuccas* in dropping their fruits as soon as mature, which was discussed in the early part of this paper, must be remembered here. In these species, *baccata*, *valida*, and *Guatemalensis*, the reflexed leaves could hardly be considered as a protection to the fruits when these, as soon as they mature and become desirable, drop to the ground, — as we suspect in order to be gathered and eaten by certain of those animals which cannot climb the trunk, the core serving to protect

* Merriam, C. Hart, "Notes on the Geographical and Vertical Distribution of Cactuses, Yuccas and Agave in the Deserts of Southern California * * * etc.," l. c., p. 353.

the seeds. In *aloifolia*, where there is no core and the fruits remain persistent until they dry up, it may be that the protection afforded the fruits by the reflexed leaves is of considerable importance. All indications here point to the fruit as being particularly modified for dissemination by small birds. The sweet tender pulp would be a tempting morsel for many animals, and not having a protecting core many of the seeds might be destroyed.

The service which the reflexed leaves render in seed dissemination has already been discussed. I would not consider, however, that this function has primarily had any influence in leading to the development of the habit of leaf reflexion. I am not disposed either to look upon the protection which this habit affords the fruits of certain species as being the primary cause. I am inclined to the opinion that the primary cause must be sought for among the intricate relations between light and growth, coupled with the habit of growth of the plant, the reflexion being necessary to permit the accumulated seeds and rubbish caught by the erect leaves to fall to the ground. It may be merely the common habit shown by certain Monocotyledonous plants of this nature, such as palms which have tufted tops at the ends of tall trunks. The lower leaves of such trees gradually assume a reflexed position, evidently due to the pressure exerted by the development of other leaves above and an attempt to assume the most advantageous position in relation to the light. The old leaves of palms gradually become strongly reflexed and ultimately dry up and break off, their bases frequently remaining attached for a time and then rotting away, leaving a smooth trunk. If this habit were coupled with the development of phytomeroids such as occur in *Y. aloifolia* one might reasonably expect this leaf reflexion to become periodic, corresponding to the phytomeroids.

The *Clistoyuccas*, having dry indehiscent fruits, include two species, *gloriosa* and *brevifolia*. Of the dissemination of *gloriosa* apparently nothing is known. While this plant

is common in cultivation it very seldom fruits and has not been much studied.

Brevifolia differs from other known species in having a very thick exocarp similar to that of *aloifolia* but which on maturing becomes dry and spongy instead of pulpy. What is known of the dissemination of this species is from the observations of Dr. Trelease:* "The fruits of this species fall quickly after ripening either by a distinct disarticulation or because of the brittleness of the pericarp at the base, and their rounded form and very light specific gravity render them well-developed 'tumble fruits' and point to their dissemination over the dry sands of the desert by aid of the strong winds which prevail there, the seeds being liberated ultimately by the breaking of the fragile pericarp."

The *Chaenoyuccas* or capsular species, which have dry erect capsules and light, strongly compressed seeds, are typical wind-disseminated plants. The capsules open by a gradual septicidal dehiscence from above downward and by a dehiscence for a certain distance from the top through the backs of the carpels (Plate 47, fig. 5).

The seeds are very thin and flat, ranging in thickness from .5 to 1.5 millimeters, and have a very slight wing (Plate 47, fig. 6), a flying apparatus of the simplest kind similar to that in Iris, Tulipa and Agave.† They are arranged in six rows and are gradually sifted out of the erect capsules by the shaking of the fruit cluster by the wind or animals and by the wind dipping into the open top of the cells. The device is thus to secure the gradual scattering of the seeds, a few at a time by gusts of wind, the wind serving to carry the seeds for some distance.

The peduncle of the capsular species is usually quite long, serving to raise the fruit cluster free of obstruction to some height above the surrounding vegetation. *Filamentosa* and *glauca*, the most widely known capsular Yuccas,

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* † Trelease, Wm., "Further Studies of Yuccas and their Pollination," l. c., p. 224.

† Hildebrand, "Verbreitungsmittel der Pflanzen," p. 16.

grow on prairies or in open fields, and *elata* is a plant which frequents the open mesas of the Arizona plains. Those Yuccas which are dependent on the wind for their dissemination apparently always grow in open places where the wind has free action upon them. The Sarcoyuccas on the contrary frequently grow in wooded areas, mountainous districts, etc. *Aloifolia* sometimes grows in dense hammocks. *Macrocarpa*, Prof. Toumey reports as a strictly mountainous plant, frequenting shady cañons in Arizona.* Habitat evidently has important connection with the methods of dissemination employed by the various species.

The peduncles in *filamentosa*, some time after the fruits have ripened, very commonly rot at the base and fall. This serves to empty the few seeds which may remain in the capsules at some distance from the parent plant. The peduncles in this species vary, in Florida, from 3 to 12 feet in length.

SUMMARY.

In Yuccas the three types of fruits, characterizing the different groups, correspond to three types of dissemination.

The *Sarcoyuccas*, having fleshy fruits, are probably intended for dissemination by fruit-eating animals.

In the fleshy fruits of *baccata*, *valida* and *Guatemalensis* the seeds are surrounded by a papery core similar to that of the apple. The fruits of these species drop early, probably as soon as mature. This seems to be a device to aid in their dissemination. They are probably gathered by small mammals that eat the pulp, the seeds, which are protected by the core, being discarded.

The fruit of *aloifolia*, which is fleshy throughout and persistent, is principally disseminated by the mocking bird. This is accomplished by the bird swallowing the seeds while eating the pulp. The seeds remain uninjured

* Toumey, J. W., "Notes on the Tree Flora of the Chiricahua Mountains." Garden and Forest, VIII. (Jan. 16, 1895), p. 22.

and are evacuated in good condition for germination. Many seeds are also scattered by being twitched to some distance by the bird, in freeing its bill from the adhering pulp and seeds. A tame mocking bird swallowed and evacuated 51 seeds in 4 hours. A number of these were afterwards germinated.

The trunk of *aloifolia* is prolonged by the lateral branch or branches which spring from near the base of the old fruit cluster. This branch prolongs the trunk and in turn bears an inflorescence and fruit, about two years being required usually to complete the period of development. The *aloifolia* trunk in its development may thus be divided into definite stages or segments, which in the lack of a term to designate them are here called *phytomeroids*. The lateral branch which continues the stem starts to develop about the time that the fleshy fruits begin to dry up. At about the same time the erect leaves of the phytomeroid to which the fruit cluster belongs begin to reflex, and soon come to point strongly downward. The reflexed persistent leaves of the older phytomeroids become closely appressed against the stem and, pointing downward like a series of bayonets, prevent small mammals from climbing the trunk. The reflexed leaves aid as a secondary method of dissemination. Seeds and dry fruits falling on these are directed or thrown outward so that they fall at a distance of a meter or so from the parent plant.

Old fruit clusters of *aloifolia*, after the fruits have passed the stage for bird eating by drying up, are cut off by the larvæ of *Prodoxus decipiens*. The leaves of the phytomeroid to which these fruit clusters belong, have by this time become reflexed and thus do not prevent the fall of the cluster but direct it outward away from the parent plant.

The reflexed leaves by preventing animals from climbing the trunk also serve to protect the fruits from the ravages of those animals that might injure the seeds.

The protection of the fruits and aid in seed dissemina-

tion are not thought to be the primary factors leading to the development of the habit of leaf reflexion.

The primary cause which leads to the development of this habit is probably to be found in the relations between light and growth, and the necessity for some such habit to free the plant from rubbish which becomes lodged in the erect crown of rigid leaves.

Yucca brevifolia, illustrating the *Clistoyuccas*, is unique in having a light spongy fruit which falls when mature and is blown about as a rolling fruit, gradually breaking up and dropping the seeds.

The capsular Yuccas, like *filamentosa* and *glauca*, are developed for wind dissemination. They have very thin light seeds which are gradually sifted out of the capsules and blown to some distance by the wind.

The wind disseminated Yuccas grow in open places where the wind can have free action upon them.

The rotting off at the base and falling of the old fruit stems of *filamentosa* serves finally to throw out all seeds which remain in the capsules.

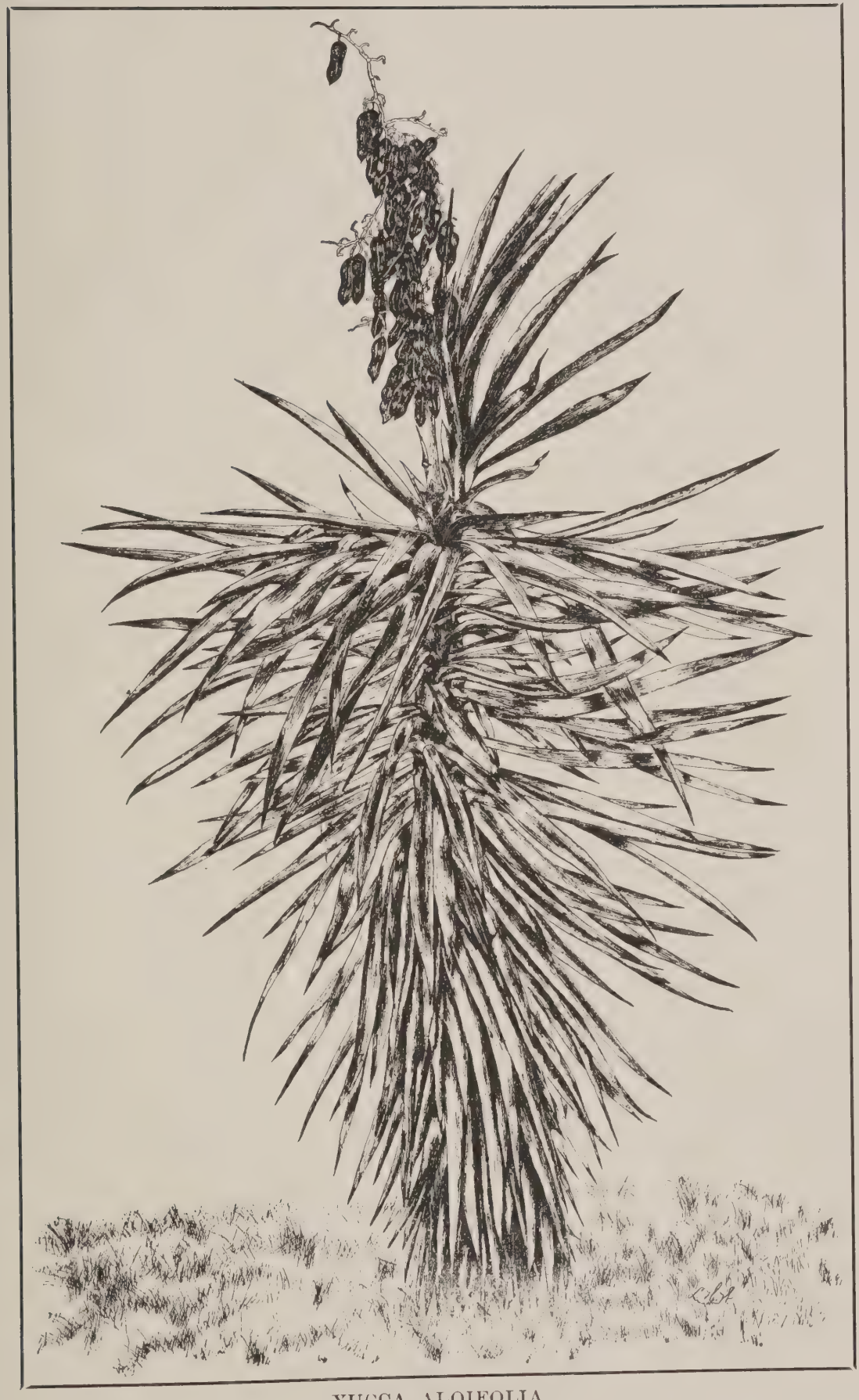
Eustis, Florida. January 12th, 1895.

EXPLANATION OF PLATES ILLUSTRATING THE DISSEMINATION OF YUCCA.

Plate 45.— *Yucca aloifolia*, with lateral branch developing from near the base of the peduncle. The leaves of the phytomeroid which bore the inflorescence have begun to reflex.—Drawn by Mrs. Webber, from a photograph of a plant at Bartow, Florida, January 24, 1894.

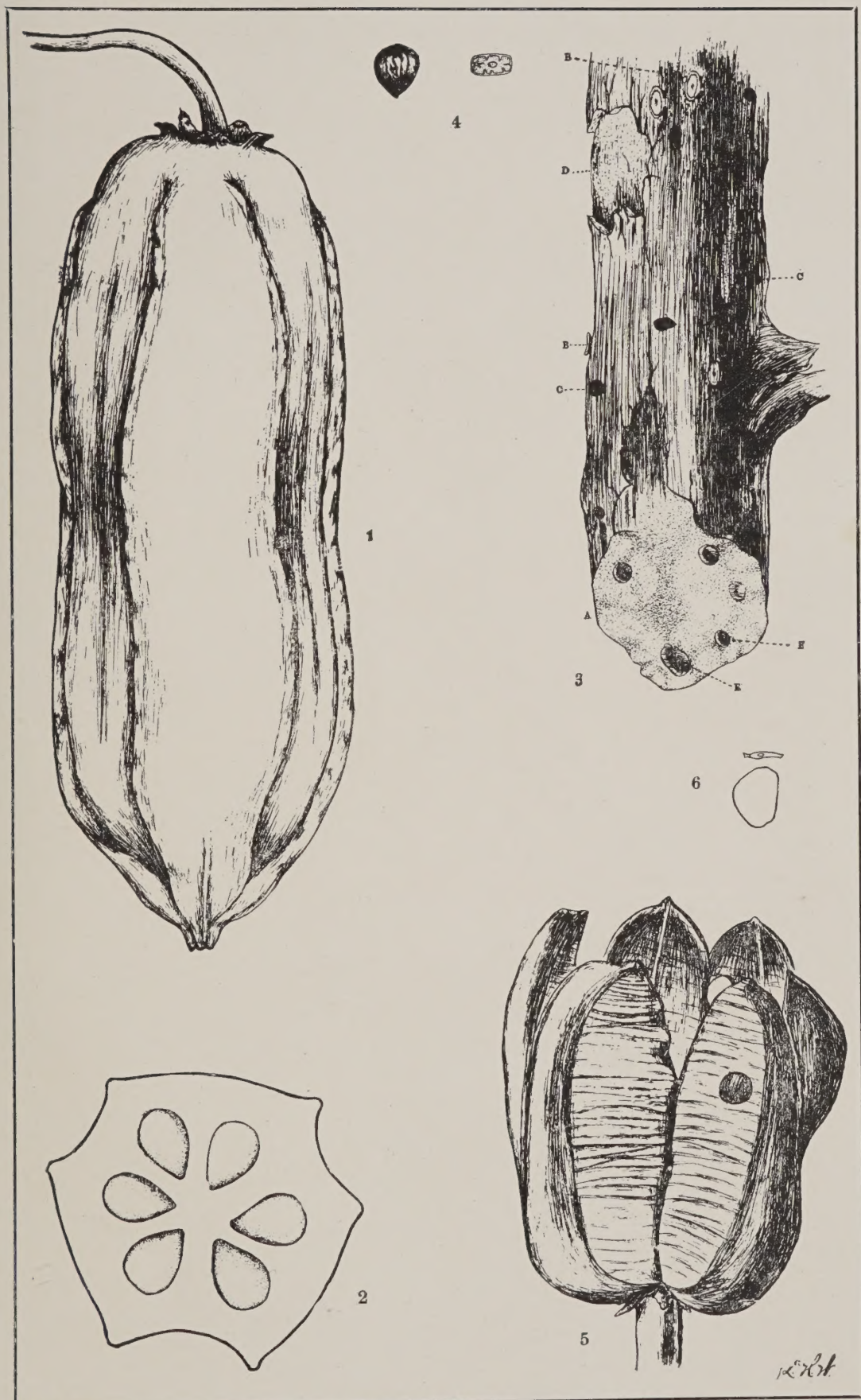
Plate 46. — *Y. aloifolia*, with lateral branches starting at the base of the old peduncles, and the leaves of the upper phytomeroid starting to reflex.—From a photograph of plants on Anastatia Island, Fla., Jan. 23, 1895.

Plate 47.—Fig. 1. Ripe fruit of *Y. aloifolia* — Fig. 2. Cross section of *aloifolia* fruit. — Fig. 3. Basal end of old peduncle of *Y. aloifolia* cut off at *a* by *Prodoxus decipiens*; *bb*, scars resulting from oviposition of *Prodoxus* female; *cc*, perforations made by the chrysalis of *Prodoxus* in issuing; *d*, portion of the epidermis cut away by the burrowing of *Prodoxus*; *ee*, tunnels in the tissue made by *Prodoxus* larvæ.— Fig 4. *Y. aloifolia* seed, and cross section of seed showing ruminated endosperm.— Fig. 5. Capsule of *Y. filamentosa*. — Fig. 6. *Y. filamentosa* seed, and cross section. — All nat. size, drawn from nature by Mrs. Webber.



YUCCA ALOIFOLIA.

YUCCA ALOIFOLIA.



YUCCA ALOIFOLIA AND FILAMENTOSA.